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GEOGRAPHIC VARIATION IN *TACHYSPHEX TERMINATUS* (HYMENOPTERA: SPHECIDAE, LARRINAE)

Nancy B. Elliott and Frank E. Kurczewski

Abstract.—Males of *Tachysphex terminatus* (Smith) were collected from a number of populations during the summers of 1968, 1969, and 1970. Color, size and punctation characteristics were compared statistically. All individuals collected east of the Rockies had red-tipped abdomens, but many individuals from the West were all black. Increased melanization of the genitalia was evident in individuals from coastal areas, both in the East and West. There was no significant size variation, except for a sample of very large individuals from coastal California, and one of small individuals from Idaho. Samples from western Kansas consistently showed lower values for vertex punctation than many of the other samples. Additional work with museum specimens from throughout the species range has tended to substantiate many of these findings.

Geographic variation in animals has been documented for external color patterns, and morphometric, chromosomal, physiological, and ecological characters. There is much literature on geographic variation in insect groups including Collembola (Christiansen and Culver, 1968 and 1969), Orthoptera (Craddock, 1970; Masaki, 1967), Homoptera (Sokal, 1952 and 1962; Sokal and Rinkel, 1963; Sokal and Thomas, 1965), Hemiptera (Slater and Knop, 1959), Coleoptera (Mason, 1964; Willis, 1967; Young, 1960), Lepidoptera (Creed et al., 1962; Lucas, 1969), Diptera (Sokoloff, 1965), and Hymenoptera (Alpatov, 1929; Michener, 1947). Within the Hymenoptera, intraspecific variation in the Sphecidae has also been treated anecdotally as by Fernald (1926) or in taxonomic revisions, as by Bohart and Menke (1963). Our paper presents results of a study of geographic variation in the digger wasp *Tachysphex terminatus* (Smith). This wasp is found throughout North America from Alaska to Mexico, except Florida, nests in bare sand, and may be locally abundant. Areas of suitable habitat are often separated by vegetation, affording the local population some degree of isolation.

Tachysphex terminatus belongs to a group of closely related North American species of *Tachysphex* including the following: *Tachysphex apicalis* Fox, *T. fusus* Fox, *T. similis* Rohwer, *T. plesia* Rohwer and *T. linsleyi* Bohart. Group members share certain diagnostic characters, including a wide least interocular distance, relatively long erect setae on the vertex, and prominent convexities behind each posterior ocellus. *Tachysphex terminatus* may be distinguished from other group members by the following set of characteristics: a ratio between least interocular distance and head width of .29–.33, a smooth punctate frons, and an unnotched

Fig. 1. Collection localities for males for 1968, 1969 and 1970. (01) Scullville, New Jersey 1968, 12; (02) New Gretna, New Jersey 1969, 16; 1970, 13; (03) Colonie, New York 1968, 13; (04) Clifton Park, New York 1969, 20; (05) Albany, New York 1970, 14; (06) Chittenango, New York 1968, 24; 1969, 23; 1970, 20; (07) Presque Isle, Pennsylvania 1968, 7; (08) Wamego, Kansas 1969, 14; 1970, 15; (09) Lakin, Kansas 1968, 12; (10) Kendall, Kansas 1969, 25; 1970, 11; (11) Hoback Junction, Wyoming 1970, 8; (12) St. Anthony, Idaho 1970, 18; (13) Mendocino Co., California 1970, 19.

clypeus. The behaviors of several species in the *T. terminatus* group have been studied by Kurczewski (1964, 1966), allowing correlation with findings on other aspects of their biologies. There are indications that patterns of geographic variation could complicate taxonomic studies of the group. Western individuals of *T. terminatus*, for example, appear superficially different from their eastern conspecifics. The range of morphological variation in each species is unknown, and it is desirable to study the extent of variation in each, before undertaking further ethological or taxonomic studies.

Methods and Materials

Adults were collected during the summers of 1968, 1969, and 1970. Collection localities are shown in Fig. 1. Preliminary comparisons between successive generations in a single locality (Chittenango, New York) in 1968 revealed significant mean differences in several characters for females, but not for males (Elliott and Kurczewski, 1974a). Since seasonal variation might complicate the study of geographic variation, only males

were collected for the remainder of the study. Specimens from museum collections were used to supplement data based on field-collected specimens for localities from which samples of five or more males were available. The collections localities for museum specimens and the number of specimens for each locality are as follows: Ithaca, New York (23); southern New Jersey (24); Riley and Pottawatomie Co., Kansas (13); Wisconsin (19); Lewisville, Arkansas (12); Kill Devil Hills, North Carolina (13); Virginia (10); Galveston, Texas (12); Mendocino Co., California (5); San Francisco, California (18); Lassen Co., California (9); St. Anthony, Idaho (6); southern Quebec (12).

Measurements and counts on specimens were made using a binocular dissecting microscope with a grid and ocular micrometer. A factor analysis on 18 morphometric characters indicated head width was a good indicator of general size. Of the characters which loaded heavily in size, it was the easiest to measure accurately (coefficient of reliability = .999 for remeasurements). For this reason it was compared as a general size measure throughout the remaining analyses. Puncture counts per grid unit on the vertex were transformed for statistical analysis by computing the mean of the square root of the two counts on each individual. Genitalia were removed from males collected in 1970, mounted on slides, and the color of the volsella, coded on a scale from 1–3 (light–dark), was recorded. The percent of each sample with red-tipped abdomens was also recorded.

Variation between annual samples was tested with one-way analysis of variance for size-related characters and puncture counts. Homogeneity of variances was first tested with Bartlett's Test (Sokal and Rohlf, 1969:370). For homogeneous variances, means were tested with Model 1 ANOVA to show actual mean differences, and variation was also partitioned into that due to variation within and between groups (Model 2 ANOVA). An F approximation was applied for unequal variances (Sokal and Rohlf, 1969: 372). Multiple comparisons were made with Student-Newman-Keuls Test (Sokal and Rohlf, 1969:242).

Results

Table 1 shows partition of variance (Model 2 ANOVA) for samples and years. During 1968 and 1969, when all samples were collected east of the Rockies, there was no significant size-related variation. In 1970, when populations from the West were also included, the Model 1 ANOVA indicated significant differences for head width ($F = 9.55$; $P < .05$). The distribution of probit means for head width in 1970 is shown in Fig. 2A. This distribution was characteristic of those for a number of size-related characters (Elliott, 1971). The lowest mean value, that for a sample from St. Anthony, Idaho, was significantly different from those values for

Table 1. Partition of variance in *Tachysphex terminatus*.[1]

Characters	% Variance (localities)	% Variance (individuals)
1968		
Head width	1.05	98.90
Punctation/vertex	34.35	65.65
1969		
Head width	.64	99.35
Punctation/vertex	26.00	74.00
1970		
Head width	37.36	62.64
Punctation/vertex	12.15	87.85

[1] Summaries of ANOVAs may be obtained from senior author.

all other samples except the one from southern New Jersey. The highest value, from Mendocino Co., California, was significantly different from all others, except that from western Kansas. Museum samples showed similar trends in geographic variation ($F = 3.34$; $P < .05$; see Fig. 2B). But differences in sample size made it difficult to demonstrate statistical significance in the multiple comparisons tests. Means for head widths for specimens from Mendocino County still ranked among the largest, along with those for specimens from Wisconsin and Quebec. Many of the smaller specimens were from St. Anthony, Idaho. Some of the larger males among the museum specimens were from Mendocino Co., California, while some of the smallest came from nearby San Francisco.

Vertex punctation varied significantly during all years of the study (in 1968, $F = 8.77$; $P < .05$; in 1969, $F = 7.70$; $P < .05$; in 1970, $F = 2.96$; $P < .05$). (See Fig. 3.) In 1968, samples from Colonie, New York and Presque Isle St. Park, Pennsylvania, had the lowest mean values for this character. These values were significantly different from those for central New York samples. A low mean value for this character in the sample from western Kansas was significantly different from the means from central New York samples. In 1969, the western Kansas sample had a significantly lower value for this character than all other samples. In 1970, the sample from this locality again had the lowest mean value for the character, and a sample of individuals from St. Anthony, Idaho had a significantly higher mean value for the character than all other samples.

All specimens collected in the East during 1968 and 1969 had red-tipped abdomens. In 1970, a number of all black males were collected from the West. None of the males from Mendocino Co., California were red-tipped;

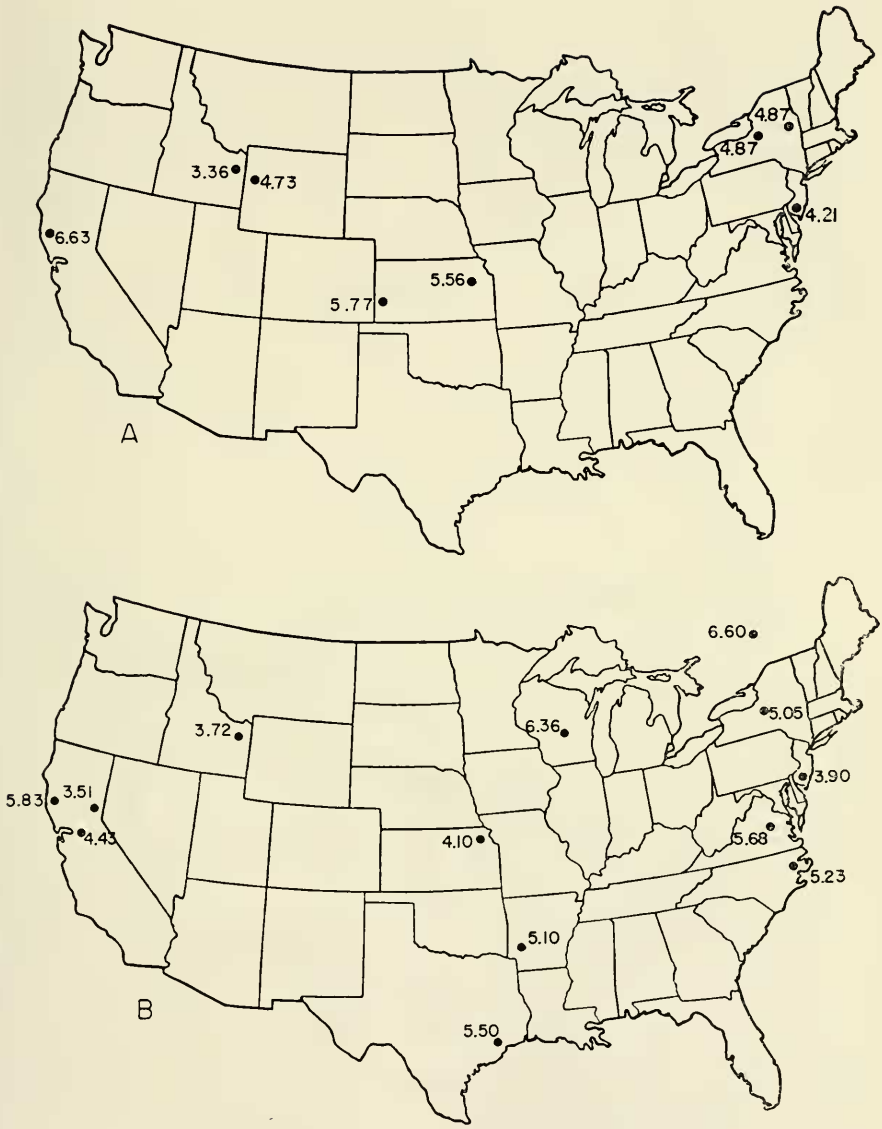

Fig. 2. Size variation in *Tachysphex terminatus* males.

A. Distribution of probit means for head width in 1970 samples. SNK Test: 3.36 4.21 4.74 4.87 5.56 5.77 6.63

B. Probit means for head width in museum specimens. SNK Test: 3.52 3.72 3.90 4.10 4.43 5.05 5.10 5.23 5.50 5.68 5.82 6.36 6.60

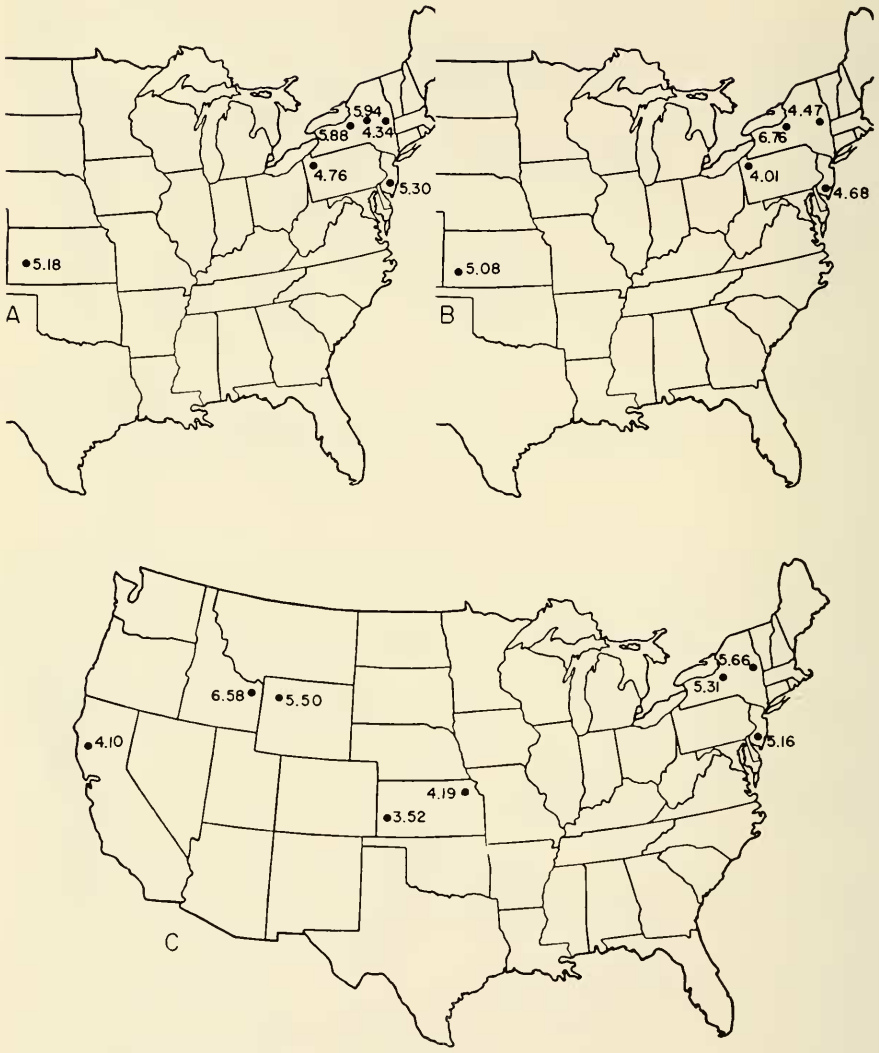

Fig. 3. Probit means for vertex punctation.

A. 1968 samples. SNK Test:
3.89 3.94 5.50 5.82 5.84

B. 1969 samples. SNK Test:
3.34 4.75 4.85 5.28 5.40 6.38

C. 1970 samples. SNK Test:
3.52 4.09 4.20 5.16 5.31 5.50 5.66 6.59

Fig. 4. Percentages of 1970 samples with red-tipped abdomens.

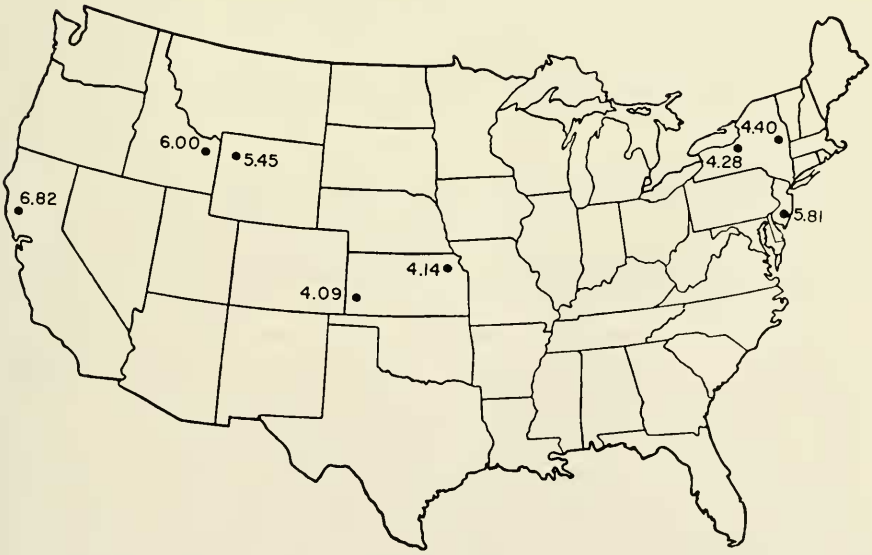

Fig. 5. Distribution of probit means for volsella color (1970).

56% of the Idaho males and 12% of the males from Wyoming were red-tipped. Figure 4 shows the distribution of red-tipped males in the 1970 field samples. Similar patterns were evident in museum specimens. All males from the East were red-tipped, whereas males from western localities were frequently all black. Among museum specimens, there were no red-tipped males from St. Anthony, Idaho or Mendocino Co., California, while 63% of the males from Lassen Co., California and 11% of those from San Francisco were red-tipped.

All black specimens showed the greatest degree of melanization on the volsella, with those from coastal California having the darkest volsellae (Fig. 5). The greatest melanization in red-tipped males occurred in specimens from coastal New Jersey. In fact, they showed more melanization than all black males from Wyoming.

Discussion

The most distinctive geographic patterns in size variation showed in samples collected in 1970. Excluding the samples from Idaho and Wyoming, there seemed to be a cline of increasing size from the smallest individuals collected near coastal New Jersey to the largest individuals from the California coast. Specimens from Idaho and Wyoming, which were smaller than those from other localities, seemed to show a second effect acting upon size, possibly related to altitude. These localities had the highest altitudes of any sampled (4,900′ and 6,000′, respectively). Thus an inverse relationship between size and altitude appeared to be superimposed on the general clinal pattern of increasing size from east to west. While no distinct longitudinal cline of size showed up in museum samples, the inverse relationship between size and altitude was indicated. The smallest specimens came from Lassen Co., California, at an altitude of approximately 5,000′. The fact that specimens from western Kansas consistently exhibited relatively sparser vertex punctation than those from other areas seemed to indicate selection acting on this or a related character. High density in vertex punctation in the Idaho specimens, which were the smallest individuals, suggested a predictable inverse relationship with size. The most obvious variation in *T. terminatus* was in abdomen color. Western males were often all black, although females occurring with them were frequently red-tipped. Males from coastal California conformed to the stereotype of specimens from coastal climates (see Fernald, 1926). They were large and dark with much melanization on the volsella. Coastal New Jersey wasps, although smaller and red-tipped, also showed increased melanization on the volsella, presumably an effect of moist coastal climates. Elliott and Kurczewski (1974b) have already reported that the presence or absence of potential competitors in the habitat may affect the morphology of related *Tachysphex* species. The

present study suggests that a number of environmental factors act independently to produce morphological variation throughout the range of *T. terminatus*. These factors may include effects of altitude in relation to size, humidity to increase melanization in coastal environments, and various effects acting on punctation characteristics throughout the range.

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Department of Entomology, SUNY College of Environmental Science and Forestry, Syracuse, New York 13210.

Present address.—(NBE), Department of Biology, Hartwick College, Oneonta, New York 13820.

NOTE

NEW SYNONYMY IN *NERTHRA* SAY (HEMIPTERA: GELASTOCORIDAE)

Two specimens of predaceous bugs of the family Gelastocoridae intercepted in Miami, Florida in an air shipment of ferns from Colombia on 22 August 1975 by F. Matthews confirm a suspected synonymy (Todd. 1955. Univ. Kans. Sci. Bull. 37(1), no. 11, p. 389). The specimens, a male and a female, represent respectively *Nerthra ater* (Melin, 1929) and *Nerthra rudis* (Melin, 1929) described in Zoologiska Bidrag Fran Uppsala, Band 12, p. 185 and p. 182. In 1955 I suggested that if the two names did apply to the two sexes of one species, *Nerthra ater* (Melin, 1929) would fall as the junior synonym. This comment was based on the concept of page priority current at that time. Since the shape of the male paramere is a better recognition character than the overlapped basal part of the right ovipositor lobe of the female, I place *Nerthra rudis* (Melin, 1929) as the junior synonym of *Nerthra ater* (Melin, 1929) [New synonymy].

E. L. Todd, *Systematic Entomology Laboratory, IIBIII, Agric. Res. Serv., USDA, c/o U.S. National Museum, Washington, D.C. 20560.*